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BIOLOGICAL BULLETIN

THE TEMPORAL ARCHES OF THE REPTILIA.

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Students of herpetology are indebted to Professor Henry F. Osborn for a careful taxonomic and morphological study [1] of the extinct reptilia, from which he has concluded that the class is divisible into two distinct subclasses or phyla, which he has called the Synapsida and Diapsida. The writer has studied his paper with much interest and desires to acknowledge his indebtedness to it for many new ideas and stimulating suggestions, though he is forced to differ from the author in some of his conclusions. A full discussion of this paper is not possible at the present time, and the present communication, will, therefore, be restricted to a discussion of the relations of the bones of the temporal arches of the reptilia, relations which really lie at the basis of any classification.

I may mention, however, that I do not see my way clear to accept the term Synapsida proposed by Professor Osborn for the group of single barred reptiles, since this group really does not differ in any essential respect from the Synaptosauria (in the wider sense) of Fürbringer [2] and differs from the Synaptosauria of Cope, as most recently defined by him [3] chiefly in the inclusion of the Cotylosauria. But, I believe that Cope was right in separating the two groups, since he recognized, as does Osborn, the ancestral relations of the Cotylosauria to both the single and double-barred reptiles. If all other reptiles are derived from them, and

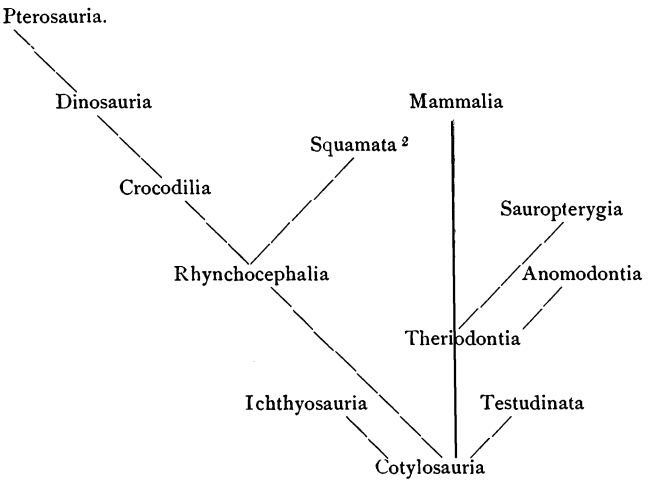
[1] "The Reptilian Subclasses, etc." *Mem. Amer. Mus. Nat. Hist.*, Vol. I., p. 451, 1903.

[2] *Jena Zeitschr.*, 1900.

[3] "The Crocodiles, Lizards and Snakes of North America," Rep. U. S. Nat. Mus., 1898, p. 159.

if the differences of these reptiles are sufficiently great to separate them into distinct orders, it would seem proper to distinguish the Cotylosauria from both the Synapsida and the Diapsida. Indeed Professor Osborn himself excludes them from union with either group in some of his definitions.

Furthermore, I cannot accept the conclusion as definitely proven, or even probable, that the reptiles are really diphyletic. The turtles seem, with much reason, to have had an independent origin from the cotylosaurs. My views in general of the pylogenetic relations of the orders of reptiles are pretty well expressed in the following diagram published by Cope in 1896.[1] It will be



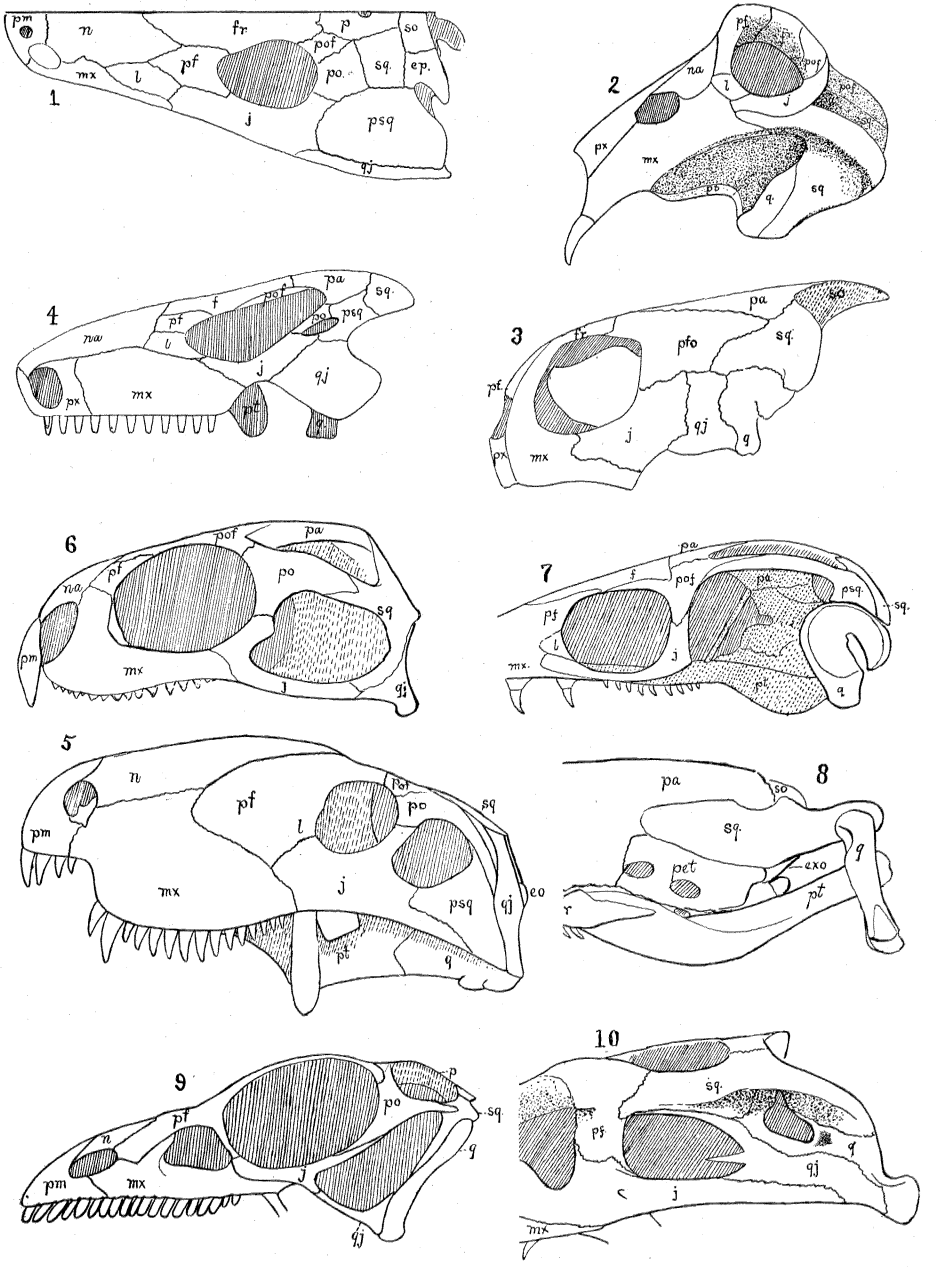
seen that, with the exception of the Ichthyosauria and Testudinata, the phylogeny scarcely differs from that of Professor Osborn, save in details. Osborn's characters are as follows:

Synapsida. — "A single large supratemporal fenestra; laterotemporal fenestra rudimentary or wanting. Bony elements of upper and lower arches not separated. Upper arch tending to degenerate first.

"Squamosals and prosquamosals large, expanded, early coalesced, forming a portion of the occiput, suturally covering the quadrate, secondarily entering the glenoid fossa.

[1] "Primary Factors of Organic Evolution," p. 115.

[2] "It is uncertain whether this order originated from the Theriodontia or the Rhynchocephalia." In the original it is derived from the Theriodontia.



1. *Mastodonsaurus*,
2. *Lystrosaurus*,
3. *Chelone*,
4. *Procolophon*,
5. *Dimetrodon*,
6. *Sphenodon*,
7. *Platecarpus*,
8. *Python*,
9. *Anchisaurus*,
10. *Gavialis*.

Diapsida.—" Large supra- and laterotemporal fenestræ ; laterotemporal fenestra sometimes secondarily closed. Bony elements of arch widely separated. Lower arch tending to degenerate first.

"Squamosals and prosquamosals often reduced, more generally separate, partially covering or withdrawn from the quadrate."

The closed or nonfenestrate condition of the temporal region has long been recognized as a primitive character in the reptilian skull. Cope, Baur and Seeley, and other authoritative writers have repeatedly called attention to the striking resemblances in the arrangement of the bones forming this region in some of the early reptiles and the Stegocephalia. Largely because of this resemblance some authors have urged the reptilian nature of the Stegocephalia, either uniting them with the reptiles as a branchiate division of the class, or placing them in a distinctive class, as " Proreptilia."

While these elements are so nearly alike in the stegocephs and cotylosaurs as to leave no doubt of their homologies, in the higher or more specialized reptiles the changes have been so great that the identification of some of the bones is doubtful. As a result of this uncertainty, many names have been proposed for the different temporal elements, aside from the postfrontal, postorbital and jugal, about which there has been no doubt or dispute. For the other four bones, however, I find the following names in use within recent years : epiotic, os tabulare, paroccipital plate, squamosal, prosquamosal, suprasquamosal, supratemporal, mastoid, supramastoid, supraquadrate, paraquadrate, zygomatic, quadratojugal, squamosal I., squamosal II. At the present time, the terms squamosal, prosquamosal, quadratojugal and epiotic seem to have most acceptance, though supratemporal is largely used for prosquamosal.

The temporal bones in the Stegocephalia and Cotylosauria are practically identical in number and arrangement (Figs. 1, 11). In both these forms it will be observed that the squamosal articulates broadly in front with the postorbital or postfrontal ; on the inner side with the parietal ; on the outer side with the prosquamosal, and sometimes the jugal. The prosquamosal unites broadly in front with the jugal ; on the outer side with the

quadratojugal. The quadratojugal has only a slight union with the jugal. The postfrontal joins by its whole length with the parietal. Now, no one will question but that this arrangement of these bones is the primitive one for the reptilia, and any rearrangement or readjustment must be a secondary result or specialization.

Among the higher forms, the nearest approach to this condition is seen in the testudinate skull (Fig. 3), in which the bony roof still remains unpierced; that is, there is no supra- or latero-temporal fenestra in such forms as *Chelone*, an undoubted primitive type of testudinate skull. The postorbital and postfrontal

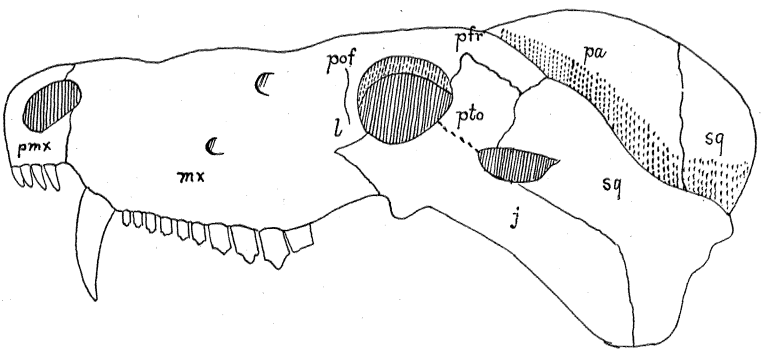


FIG. 14. *Cynognathus*, after Woodward.

are not distinct, or one or the other is absent. The prosquamosal has disappeared, or has become fused with some adjacent element. The quadratojugal has become greatly enlarged, separating the jugal from the quadrate, and articulating above with the squamosal — that is, it has taken the position of the prosquamosal in the *Pareiasaurus* skull. It is assumed that the prosquamosal, if present, is fused with the squamosal, but I fail to see any conclusive evidence of this; and it would seem more reasonable that, if the element is really present in the testudinate skull, it is fused with the quadratojugal, which has usurped its place and relations. Indeed the loss of the narrow bone on the outer side of the cotylosaurian skull would leave an arrangement pretty similar to that of *Chelone*, except that the quadrate is partly uncovered.

In the posterior part of the skull a vacuity has arisen, or, more

probably, was inherited from the cotylosaurs, between the parietal, paroccipital and squamosal, the posttemporal vacuity. By an emargination of the roof from behind, the squamosal may become separated from the parietal, and by an emargination from below,

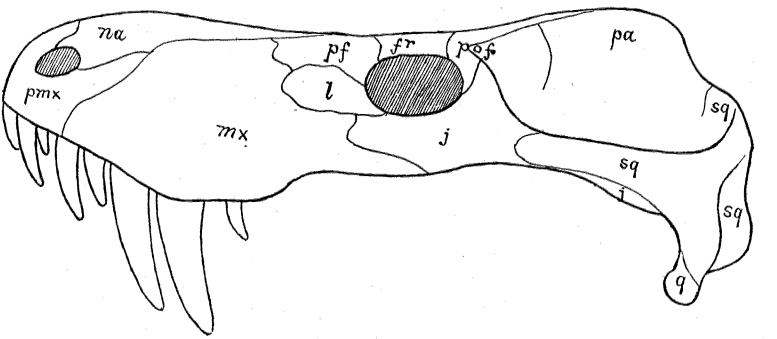


FIG. 12. *Lycosuchus*, after Broom.

from the postorbital, indeed, entirely isolating it in the arch. In such cases a large fossa is disclosed from above, which is sometimes, *though incorrectly*, called the supratemporal fossa. Baur some years[1] ago called attention to the fact that the turtles have no supratemporal fossa or fenestra. In fact, the temporal roof of the turtles throughout seems to be quite like that of the cotylosaurs, judging from Seeley's description:[2] "While the temporal vacuities are roofed over in *Pareiasaurus*, the roof is like the primitive roof of the genus *Chelone*, whereas in Professor Cope's figures of *Empedias* the skull appears to be closed behind as in Gorgonopsia." That the turtles ever had a supratemporal fenestra is quite out of the question. How, then, is it possible to derive them from the Anomodontia (*sens. lat.*), or from any known group of reptiles save the Cotylosauria? The entire absence of the quadratojugal bone, or any ossification corresponding to that bone in the Testudinata, in all the Anomodontia, Theriodontia, Placodontia and Therocephalia is exceedingly difficult to explain, if they are ancestral to the turtles. Has this bone reappeared, after its loss or close fusion with other bones? I am aware that many attempts have been made to show the relation-

[1] *Jour. Morph.*, iii., p. 472, 1889.
[2] *Phil. Trans.*, 1894, p. 1009.

ship of the turtles with the placodonts and plesiosaurs, but a study of these forms convinces me that whatever resemblances they may present can be accounted for by parallel development. Briefly, there are other characters in the skeleton that seem inconsistent with such a derivation from the Anomodontia, the intercentral attachment of the ribs, the presence of parial intercentra in the cervical vertebræ of some forms, etc. The conclusion seems irresistible to me that the Testudinata represent a distinct phylum of the reptilia, coördinate with the Synaptosauria or Synapsida.

By a sort of natural trephining of the skull-wall, a vacuity appeared between the squamosal and parietal, the squamosal still retaining its connection posteriorly with the parietal, and the

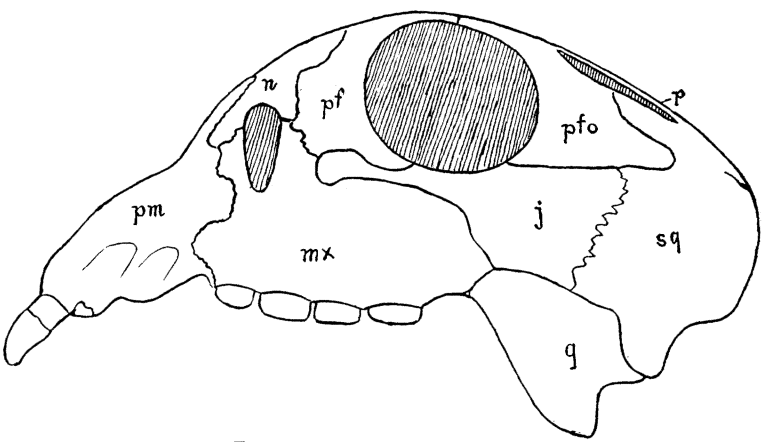


FIG. 13. *Placodus*, after Meyer.

postorbital taking a part in the separated bar thus formed. This is the condition in the Anomodontia and Sauropterygia, but never in the Testudinata. In the Anomodontia and Sauropterygia, concerning whose relationships there can be no doubt, the prosquamosals and quadratojugals have disappeared, leaving a single bar composed of the squamosal, postorbital and jugal. It is also assumed here that the prosquamosal and perphaps also the quadratojugal have become fused with the squamosal, but of this there is not a scintilla of evidence. A separate ossification, it is true, has been said to occur in some plesiosaurs by Owen,[1] which

[1] *Trans. Geolog. Soc. Lond.* (2), V., pt. iii., pl. XLV., 1840.

might be supposed to be the prosquamosal, but in the excellent skulls of four genera of these animals which I have examined there is positively no such separate element present, nor was there any recognizable prosquamosal present in the skulls described by Andrews. Nor has such an element ever been recognized in the Nothosauria. I am aware that Koken[1] has suspected the presence of such an element in one specimen of a nothosaur, but his evidence was very doubtful and has not been confirmed. I am confident that the true squamosal in these groups, as in the cotylosaurs and turtles, articulates directly with the post-

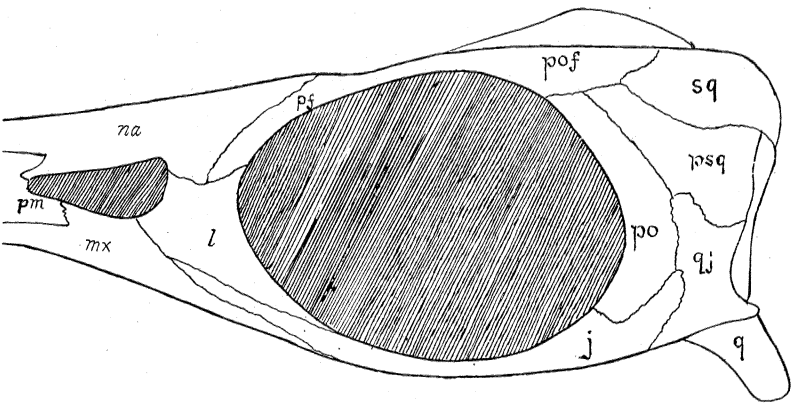


FIG. 17. *Ichthyosaurus*, after Owen.

orbital and jugal, without the intervention of any other element, and that the prosquamosal is wanting, not fused with adjoining bones; nor is there any certain evidence of the presence of the quadratojugal in any of these reptiles. In certain plesiosaurs I have found and figured what I believed to be a distinct ossification — a small, perhaps rudimentary one — that I took to be the quadratojugal. But I have never been able to trace it out, and no other observer has ever distinguished this element in the Sauropterygia. In the Anomodontia no such element has been certainly found, and, since we have the best of reason for believing that the anomodonts and theriodonts are closely related to the ancestors of both the nothosaurs and the plesiosaurs, we can hardly expect to find the bone distinct in these latter forms.

[1] *Zeitschr. Deutsch. Geolog. Gesellsch.*, XLV., 1893; p. 362.

Since the above was written, I have received the following statement from Dr. Broom, kindly sent in reply to a query from me: "No trace of either prosquamosal or quadratojugal has been found in any Anomodont or Theriodont. The large bone which supports the quadrate in *Dicynodon* and also forms so large a part of the temporal arch is all pure *squamosal*. The same is the case in the Therocephalia and Theriodontia. The upper part of the quadrate which rests on the squamosal has been thought by some to be the quadratojugal, but I am pretty confident that the whole is quadrate, and that no rudiment even of the quadratojugal is present."

From these facts we may conclude that the emargination of the single bar has removed all of the lower arch, and that all which remains corresponds to the upper arch of the diapsid reptiles, the squamoso-postorbito-jugal bar. Certainly until some form is discovered in which the prosquamosal and quadratojugal are definitely shown to be present as a part of the arch, the compound nature of the arch in the synapsid forms is hypothetical. One species of *Cynognathus* has been figured (Fig. 14) with a small fenestra between the squamosal and jugal. No other species of this genus possesses this opening, and its presence in this species, is, I believe, disputed by Dr. Broom. Even if it be present, it has no classificatory significance, since it must have been a parallel development in these animals; an abortive attempt, as it were, without phylogenetic significance. It is of interest, perhaps, if it really occurs in any of the anomodonts, as showing the tendency to perforation of a broad plate covered on both sides by muscles.

The question is properly asked: How has the mammalian zygoma arisen? The answer does not seem doubtful to me. The mammalian arch has the structure of that of *Lycosuchus* (Fig. 12), and is composed of the squamosal and jugal alone. This it seems to me, will be made apparent by the consideration of the arch in *Placodus* (Fig. 13), *Cynognathus* (Fig. 14), and *Lystrosaurus* (Fig. 2), in which the articulation of the squamosal is with both the postorbital and the jugal in about equal measure.[1]

[1] "I can find no difference in the character of the arch in the Anomodontia and Theriodontia except that in the Theriodont the malar bone has a greater external back-

In all the plesiosaurs (Fig. 16) the union of the squamosal with the postorbital has become much reduced, they merely touching each other and approaching the theriodont type, in which the postorbital has become wholly separated from the squamosal (Fig. 12).

The assumption that the prosquamosal or quadratojugal has thrust itself up between the squamosal and the postorbital is gratuitous, without evidence to support it. And, if they have not been thrust upward into this intercalary position, it must be assumed, if the bones are really present, that they form the lower part of the bar, parallel with the squamosal, intercepting the jugal from union with the squamosal. That the jugal may unite with the squamosal, even when the prosquamosal exists as

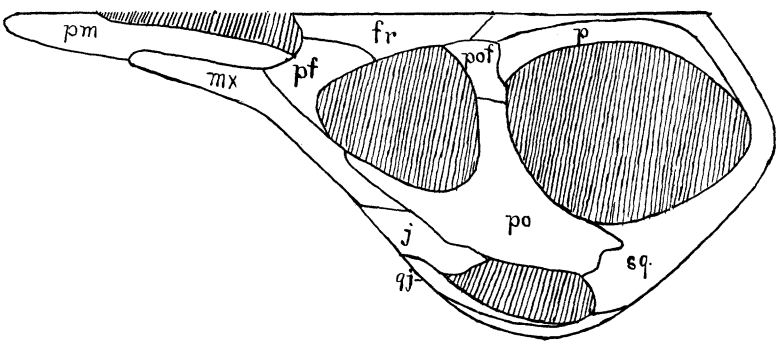


FIG. 15. *Stenometopon*, after Boulenger.

an independent ossification, is a fact, as is shown by the structure in the cotylosaur skull. Why then is it necessary to assume that these bones, or either of them, are present in the anomondonts and sauropterygians in a fused condition?

It is of course possible that the quadrate has also become a part of the mammalian arch, as has been urged by Dollo, Albrecht, Baur and others. The extraordinary development of the squamosal bone in the anomodonts and theriodonts has not only crowded out the prosquamosal and quadratojugal, but has also caused the absorption of the quadrate, enclosed between it and

ward development than is usually seen in the Cynodontia; but the difference between the groups is not due to any difference in the nature of the arches, but to a less development of the quadrate bone in the Theriodontia, which has resulted in a diminution or atrophy of the descending pedicle of the squamosal bone" (Seeley, *Phil. Trans.*, 1894, p. 997.)

the skull wall, the squamosal taking its function as an articulating bone for the lower jaw. I see no urgent reason for insisting that a vestige of it must yet be present in the eutherian skull, either as a part of the zygomatic arch, or in a totally different function as one of the ear bones. We are quite sure that some of the bones of the reptilian skull are not present in the mammalian skull, why may not the quadrate be one of them? There seems to be an idea that bones of the reptilian skull can only become lost by their union with contiguous bones, their ossific centers finally disappearing. But I am skeptical of this. We know that the quadratojugal is not present in the Squamata; that the 'prosquamosal' of the arched lizards is not present in

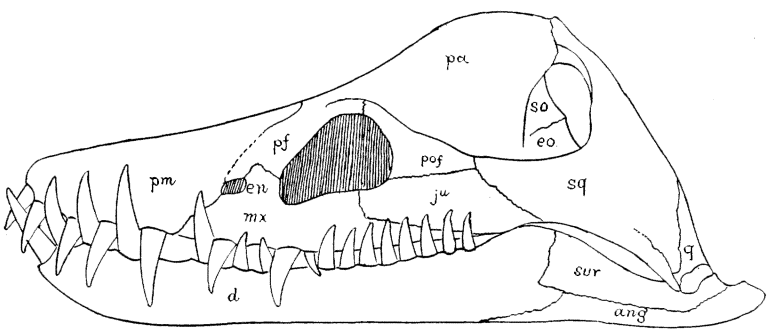


FIG. 16. *Cimoliasaurus*, original.

the amphisbænians or snakes; that the epipterygoid is also wholly wanting in some of the lizards, as well as other bones. Must we insist that their loss has always been by fusion and loss of ossific center? Must we insist that the lachrymal bone is always present in the turtles, snakes and *Sphenodon*; that the jugal is still a part of the postorbital or maxilla of the snakes; that the prevomers still remain as a part of some other bones in the eutherian mammals; that the splenial and coronoid still remain in the mammalian mandible?

Turning now to the double-barred or diapsid forms, it is a question which of the two vacuities appeared first, or whether they did not appear together. In *Ichthyosaurus* and *Aëtosaurus* we have a single vacuity, but the relations of both these forms are so evident with the early rhynchocephaloid reptiles that

there is perhaps good reason for the belief that the original lateral fenestra in the icthyosaurs has become closed up by the posterior obtrusion of the orbit, as was suggested by McGregor. That this was really the case, however, has by no means been proven. We can conceive of an early diapsid stem without lateral fenestration (as is indeed the case, in *Procolophon*), from which the ichthyosaurs might have been derived. Certainly the Ichthyosauria are the most primitive of reptiles, save the cotylosaurs, in so far as the lateral temporal region is concerned. The squamosal and postfrontal here form the outer boundary of the supratemporal vacuity, while the large prosquamosal is intercalated between the squamosal, postorbital and quadratojugal. If the ichthyosaurs originally had a latero-temporal fenestra it was situated, in all probability, above the prosquamosal. (Fig. 17.)

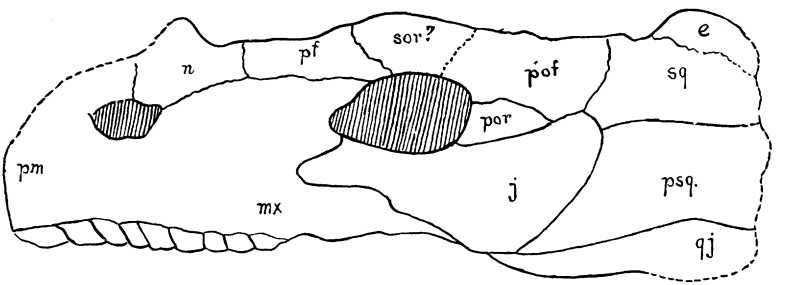


FIG. 11. *Pareiasaurus*, after Seeley.

Next to the ichthyosaurs, the most primitive of the diapsid types, as urged by Broom and Osborn, seems to be *Procolophon.* (Fig. 4). Here there is a peculiar arrangement of the bones of posterior region. A slender one by the side of the frontal and parietal, above the orbital opening, must be the postfrontal; while another bone articulating with the parietal and jugal, situated below and behind the eye cavity, is as certainly the postorbital. The orbit, we may conclude, has been extended backward, not by the closing up of the laterotemporal vacuity, but by the absorption of the postfrontal and postorbital, so as to come into contact with the parietal between them. But the orbit does not include the supratemporal vacuity, since neither the postorbital nor the squamosal helps form its outer boundary. There

is no evidence, in my opinion, that the large eye-opening has been formed by the coalescence of the supratemporal and orbital vacuities, but rather by the extension backward of the orbit, through the absorption of the postorbital bones. At the posterior part of the skull is seen an element which was believed by Seeley [1] to be the epiotic, a bone otherwise unknown, save possibly in some anomodonts, in the higher reptilia. Woodward, [2] however, identifies this bone as the squamosal, and the so-called squamosal in front of it he cails the prosquamosal. I do not feel at all sure which view is correct. If the two elements are really the epiotic and squamosal of the cotylosaur skull, I fail to understand how *Procolophon* could have stood in any very intimate relations with the early rhynchocephaloid reptiles, for they primitively had a prosquamosal. Professor Osborn states that all the elements of the cotylosaur skull are present in *Procolophon*, but neither his figure, nor Seeley's nor Broom's descriptions indicate the presence of all three bones, the epiotic, squamosal and prosquamosal — one of these elements seems certainly to be absent. Between the postorbital and the squamosal, there is a small vacuity shown in the original figure of this reptilian skull, the one reproduced here, which has been believed to be the laterotemporal fenestra. But, if I am correct, Dr. Broom denies the presence of this opening, and the figure he has been kind enough to send me shows no laterotemporal vacuity, in that position at least. Are we to suppose, such being the case, that, in addition to the absence of a supratemporal vacuity, the lateral opening also has been closed up secondarily? It seems to me that such reasoning savors a little too strongly of the ante-Baconian methods.

While *Procolophon* is shown by Broom, from certain evident peculiarities of the skull and skeleton to be more nearly related to the Rynchocephalia than to the Anomodontia, I fail to see any striking resemblances in the temporal region. It is a diapsid without temporal fenestræ.

Perhaps the most primitive known of the truly rhynchocephaloid type of reptiles, so far as the temporal region is concerned,

[1] *Phil. Trans.*, 1889, p. 271. "It rests by a squamous overlap upon the posterior border of the squamosal, and the external surface of the parietal."

[2] "Vertebrate Paleontology," p. 149, Fig. C.

is the Pelycosaurian *Dimetrodon* (Fig. 5) from the Permian of Texas, recently fully made known by Professor Case.[1] Here we have, in addition to the fully developed superior opening, a large fenestration below the squamoso-postorbital bar, and bounded below by the jugal and prosquamosal. The quadratojugal is relatively small, intercalated between the prosquamosal and the quadrate, and wholly separated from the jugal. *Paleohatteria* may possibly have a separated prosquamosal in the same position and with the same relations, but this fact, if fact it is, is yet to be determined. The Triassic *Hyperodapedon* and the allied *Stenometopon* (Fig. 15) have no separated prosquamosal. *Saphæosaurus*, from the Jurassic, more nearly ancestral, perhaps, to the modern *Sphenodon*, in all probability possesses a separated prosquamosal intercalated between the quadratojugal and the jugal, as in *Dimetrodon*. Finally in the living *Sphenodon*, notwithstanding its many primitive characters, the prosquamosal has utterly disappeared, even in the embryo, according to Howes and Swinnerton, though the squamosal is continued above the quadratojugal to unite with the jugal (Fig. 6). Here the quadratojugal articulates with the jugal, as in all the archosauria, the intervening bone having disappeared. Baur[2] believed that the prosquamosal was present in *Sphenodon* though early fused with the squamosal, a view which now is shown to be incorrect. The bone has been gone so long that it fails to make any impression upon the embryo.

From all of which evidence, *Dimetrodon*, *Saphæosaurus*, possibly *Paleohatteria*, and the conditions now existing in *Sphenodon*, the conclusion is irresistible that the laterotemporal vacuity was originally formed in the true diapsid reptiles not below, but above the prosquamosal; that this bone has nothing to do with the upper bar in these reptiles, which without exception was formed primitively by the squamosal and postorbital; secondarily by the squamosal, postorbital and jugal; finally in the theriodonts and mammals by the squamosal and jugal alone. The prosquamosal never forms the outer margin of the supratemporal fossa.

All this leads us to the consideration of the arch in the Squamata wherein the condition of things has caused no end of con-

[1] *Journal of Geology.*

[2] *Anat. Anzeiger*, X., p. 321, 1895.

troversy and differences of opinion, differences which are by no means yet settled. The single arch present (Fig. 7) has been variously considered to be the lower arch, the upper arch, or a compound of both arches. It is composed (when present) of three bones; an anterior one, the postorbital, extending backward to unite with a middle one; the middle one joining the postorbital in front, the posterior one and often the parietal behind, and more or less broadly articulating with the upper end of the quadrate; and a posterior element, joining the parietal internally, the middle element anteriorly, and united with the petrosal and exoccipital below, and usually also articulating with the head of the quadrate. The middle bone has been called the temporal, squamosal, quadratojugal, prosquamosal, supratemporal, zygomatic, supramastoid, paraquadrate; the posterior element, the mastoid, squamosal, supratemporal, supramastoid, and paroccipital. At present most writers, following Baur,[1] call the middle element the prosquamosal, and the posterior one the squamosal, though Woodward[2] applies the name squamosal to the middle element, and supratemporal (prosquamosal) to the posterior one.

It is now generally assumed that the Squamata have descended from the rhynchocephaloid reptiles. We have seen that in the early diapsid reptiles the prosquamosal is not articulated between the squamosal and the postorbital, but forms a part of the lower arch between the quadratojugal and the jugal. Here, however, it is assumed that the lower arch of the rhynchocephs has disappeared, that the quadratojugal is lost, but that the bone articulating with the quadratojugal between it and the jugal has been transferred to the upper arch, a position unknown in any other reptile, recent or extinct, to bound the outer part of the supratemporal vacuity. One could with as much reason call it the quadratojugal with former authors and with Baur[3] when he believed that the Squamata were not closely related to the rhynchocephalians, and that the arch of the Squamata was formed, not by the loss of the lower arch, but by the fusion and attenu-

[1] *Anat. Anzeiger*, X., p. 328, 1895.

[2] "Vertebrate Paleontology," p. 143, Fig. E; p. 192, Fig. A, 1898.

[3] *Journ. Morphology*, III., 473, 1889.

ation of a compound arch. One thing seems very probable, if this bone is the prosquamosal, then the Squamata have nothing to do with the rhynchocephaloids, but represent a separate and distinct phylum of their own. I prefer to call the bone articulating with the postorbital the squamosal, the bone which in all other reptiles articulates with the postorbital behind.

Of course, if this is the real squamosal, the posterior element cannot be a squamosal, though Koken [1] thought to solve the difficulty by calling the two bones squamosal I. and squamosal II. The history of the contention between Cope and Baur [2] as to the identity of this bone is too fresh in the minds of anatomists to need repeating here. Baur vigorously urged that the bone at the end of the suspensorium is the squamosal, but Baur never fully understood the relations of this bone in the mosasaurs, as is evidenced by his faulty description of it.[3] As Cope has repeatedly affirmed,[4] and as I have confirmed,[5] the so-called squamosal of the mosasaurs is intercalated between the exoccipital and petrosal, extending far inward nearly to the surface of the braincase. It needs but a moment's consideration by any one familiar with the relations of the bone in these animals and in the mammals to be convinced that such remarkably different conditions cannot be those of the same bone. The inner part of the "squamosal" corresponds quite well with the outer part of the paroccipital, or opisthotic element, which was not found in the lizard embryo by Parker. Referring now to the figures of *Procolophon* and *Pareiasaurus*, it will be seen that the outer part will correspond fairly well with the one called the epiotic. "In some of the genera of Stegocephalia the paroccipital is free from the exoccipital; in others (*Mastodonsaurus*) it is coössified with the exoccipital. The paroccipital is in relation to a dermal plate which is very improperly called the epiotic. I propose the name '*paroccipital plate*' for it." [6] It may be objected that the presence of an epiotic bone in the lizards is a far too primitive char-

[1] *Zeitsch. Deutsch. Geol. Gesellsch.*, XLV., p. 363, 1893.
[2] *Amer. Nat.*, 1895, 1896.
[3] *Jour. Morphology*, VII., p. 14, 1892.
[4] *Trans. Amer. Phil. Soc.*, XVII., p. 19, 1892.
[5] *Univ. Geol. Surv. Kans.*, IV., p. 121, 1898.
[6] Baur, *Journ. Morph.*, III., p. 469, 1889.

acter, but we are now quite certain that the lizards are an exceedingly old group, probably dating from the Permian, and that they have not a few very primitive characters, such as the presence of pterygoid teeth; perhaps the early forms, like those of the early crocodilia, will all be found to have amphicœlous vertebræ. However, whether or not this outer plate has early fused with the paroccipital beneath it, and has remained persistent in the lizards, I will not say, but I do believe that the bone corresponds to the paroccipital.

The archosaurian type of arches is one easily derivable from the Rhynchocephalia — a conjoined postfrontal and postorbital uniting posteriorly with the squamosal, to form an upper bar; and a quadratojugal intercalated between the jugal and quadrate to form the lower bar. The variations in the dinosaurs (Fig. 9) and the crocodiles (Fig. 10) are not great, and doubtless a like structure will be found in the pterosaurs when this part of their anatomy is better known than it is at the present time.

Returning now to the theses which headed this discussion, we see: That, in the Synapsida, neither the Cotylosauria nor the Testudinata have a large or any supratemporal vacuity; that, the cotylosaurs, if ancestral to the Synapsida, the Diapsida and the Testudinata, cannot be properly included into a subclass with any one of them; that the turtles could not have been derived from the Anomodontia, but apparently represent a distinct and independent branch from the Cotylosauria, or at the least from the primitive stem of the Synapsida before it had developed a supratemporal fenestra; that there is no evidence of a prosquamosal bone in any of the Synapsida (excluding the cotylosaurs), and little of the quadratojugal in the Anomodontia and Sauropterygia; that it was the elements of the lower, not the upper arch which became degenerate, leaving the mammalian zygoma to be composed of the squamosal and jugal only.

That, in the Diapsida, the prosquamosal is known to be present in but two forms; that it was an element of the lower, not the upper arch; that the arch of the lizards is the upper, not the lower one, and consequently does not contain the elements of that arch; that *Procolophon*, though a primitive diapsid, had

neither upper nor lower temporal fenestra, and probably never had.

These, it seems to me are legitimate conclusions from the evidence now available. But the evidence is yet meager, and all our present views may undergo material modification when more of the early reptiles from the Trias and Permian are known.

EXPLANATION OF FIGURES.

ep., epiotic.
exo., exoccipital.
fr., frontal.
j., jugal.
l., lachrymal.
mx., maxilla.
n. or *na.*, nasal.
p. or *pa.*, parietal.
pf., prefrontal.
pm., premaxilla.
pof. or *pfr.*, postfrontal.
po., or *pto.*, postorbital.
psq., prosquamosal.
pt., pterygoid.
q., quadrate.
qj., quadratojugal.
so., supraoccipital.
sq., squamosal.

In Fig. 4, *Procolophon*, the determination of the squamosal and prosquamosal is that of Woodward. According to the interpretation of Seeley, Broom and Osborn, *sq.* is the epiotic, *psq.* the squamosal. I am under obligations to Prof. Case for permission to use his figure of *Dimetrodon* in advance of publication by him.